

Prospects of the Use of Wild Relatives for Pea Breeding¹

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Abstract—The current global climate change results in shift and shrinkage of ranges of crop cultivation. The potential of crop wild relatives as an important source of genetic diversity for breeding is underestimated. Wild relatives of pea include the species *P. fulvum* and the subspecies *P. sativum* subsp. *elatius*, whereas wild representatives of *P. abyssinicum* are unknown. Wild peas are characterized by spontaneous dehiscence of pods and ballistic seed dispersal. The cultivated pea represents just a phyletic lineage within *P. sativum*. Pea crop wild relatives are promising with respect to: (1) resistance to pests and pathogens; (2) resistance to abiotic stress; (3) nutritional value; (4) agrotechnical advantages, e.g. branching, ability of hibernation etc.; (5) symbiotic nitrogen fixation; etc. *P. fulvum* is resistant to pea weevil, rust, powdery mildew and ascochyta blight. Some *P. sativum* subsp. *elatius* are resistant to nematodes, broomrape, powdery mildew, *Fusarium* wilt, root rot, ascochyta blight and white wilt. *P. sativum* subsp. *elatius* responds to weevil oviposition by neoplastic pustules of the pod wall controlled by the locus *Np*. Some *P. sativum* subsp. *elatius* accessions have lowered transpiration rates, and an accession from Italy survives at -20°C . Analyses of quantitative trait loci have been carried out for resistance of *P. fulvum* to pea weevil, powdery mildew and rust and for resistance of *P. sativum* subsp. *elatius* to broomrape, bacterial blight and ascochyta blight. Aryamanesh et al. (2012) obtained five introgression lines with pea weevil resistance transferred from *P. fulvum* to *P. sativum*. The practical use of wild peas is hampered by insufficient awareness of their diversity and differences from cultivated peas. Studies of useful traits of wild peas and their natural diversity, which is rapidly vanishing, should be intensified.

Keywords: *Pisum sativum*; *Pisum sativum* subsp. *elatius*; *Pisum fulvum*; *Pisum abyssinicum*; pea; crop wild relatives; resistance to pathogens; resistance to pests; QTL analysis; breeding; prebreeding; genetic diversity

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Agriculture is impossible without breeding. Even archaic productive economics implied unconscious selection in favour of the so called domestication syndrome (Hammer, 1984; Weeden, 2007). This automatically implied selection for increased productivity. The modern agriculture is based on directional selection using the wide range of methods from traditional to involving gene engineering. At present breeding is facing new goals, such as increase of productivity per arable land area unit, demanded by growing human population of the earth, and adaptation of crops to changing climate.

The global warming taking place presently (whatever be its causes) changes conditions of crop growing even in short time scale (dozens of years). It has been shown that the warming observed over the globe since 1981 to 2002 resulted in yield loss about 40 mln t (5 bln dollars) (Lobell and Field, 2007).

Little is known about reaction to warming in pea. Temperatures above $+27^{\circ}\text{C}$ decrease the yield, while those above $+30^{\circ}\text{C}$ impair seed germination. Increased

CO_2 content in the atmosphere tempers the negative effect of high temperatures to the pea plant turgor but may lower resistance of the photosynthesis to sharp warmings. The modern “semi-leafless” (missing leaflets, homozygous for mutation *af*) pea cultivars are more draught resistant (Coyne et al., 2011; Redden et al., 2011). These scarce studies were carried out on modern cultivars while nothing is known about reaction of old landraces and wild forms, especially originating from warm regions.

In a long time scale, the global warming shifts zones favourable for cultures to the north (Hatfield, 2011), climatic approximations showing that for most crops those areas will shrink (Ramirez-Villegas et al., 2013).

Any selection is based on such an important factor as the resource of initial genetic diversity. Meanwhile for most crops, the genetic diversity available for traditional selection appears just a small portion of the potentially available for a given plant species. Domestication of most cultivated plants took place in a restricted area (less frequently in several areas), from where the practice of their cultivation has spread

¹ The article was translated by the authors.

together with that initial genetic pool which was involved in the domestication event. Recently this point of view is denied by adherents of the so called “Protracted Mode of Domestication” (Tanno and Wilcox, 2006; Weiss et al., 2006; Fuller, 2007; Allaby et al., 2008; Brown et al., 2009; Glemin and Battailon, 2009; Fuller et al., 2011, 2012; Asouti and Fuller, 2012). These authors assume that domestication of crops of the Near East origin took place all over the so called Fertile Crescent territory, including the uplands of Palestine and Lebanon, Taurus, Anti-Taurus, Zagros and the basins of Jordan, Orontes and the Tigris and Euphrates headwaters, that is at the territory of about 750×1500 km, and was a gradual process lasting for about 3 thousand years. The upholders of a more traditional but somewhat exaggerated “Core Area hypothesis” suppose that domestication of the founder crops of the Near East lasted for just several hundreds of years and took place on the territory not more than 150×250 km situated in two present-day Vilayets of Turkey, Mardin and Diyarbakır, that is in Turkish Kurdistan (Lev-Yadun et al., 2000; Gopher et al., 2001; Abbo et al., 2010a; 2011a, 2012, 2013), where until now plant communities are found which include several crop progenitor species observed together at plots up to 1 square metre (Abbo et al., 2013). The hot debate between these two ‘parties’ is still going on in most prestige journals. It would be reasonable to have a look at this problem with respect the crop to which this paper is devoted, the pea.

Natural genetic diversity of not only the genus Peas (*Pisum* L.) but also immediately of the species Pea (*Pisum sativum* L.), wild representatives of which are broadly distributed in the Mediterranean and Anterior Asia, remained beyond and focused studies and pea breeding until the end of XX century. The cryptic genetic diversity of peas became evident in attempts of reconstruction of the genus phylogeny by means of molecular methods and involving wild forms. It should be noted that there were few of those. Nevertheless, data obtained from quite different molecular markers (Hoey et al., 1996; Lu et al., 1996; Ellis et al., 1998), including polymorphic retrotransposon insertions (Vershinin et al., 2003; Jing et al., 2010) and the primary structure of coding sequences of a number of structural genes (Jing et al., 2007; Zaytseva et al., 2012, 2015) showed unequivocally that the cultivated pea represents just one of the numerous phyletic lineages of the same species, while others were represented in analyses by few accessions only and, besides, were never involved into breeding. (However, all reconstructions suggest that *Pisum abyssinicum* was domesticated independently from *P. sativum* subsp. *sativum*.) A special assessment of 121 markers including isozymes and DNA-markers of the RAPD, SSR and STS-classes revealed a very low genetic diversity of European cultivars compared to a wide diversity characteristic for the species in general (Baranger et al., 2004). In particular, in that work a core collection was

suggested to contain 43 accessions having in sum 237 (96%) alleles of 245 ones revealed in all 148 studied accessions. Later a narrow genetic diversity of the contemporary cultivated pea was repeatedly reported by other authors as well (Smýkal et al., 2010, 2012).

It is very symptomatic that the maximum genetic diversity of the cultivated pea was revealed by L.I. Govorov (1928) in Afghanistan. Because of the point of view by N.I. Vavilov predominating that time, according to which the centres of a crop genetic diversity should coincide with the centres of the crop origin (Vavilov, 1926, 1927, 1929), Govorov supposed that Afghanistan was among the regions where the pea entered cultivation. Meanwhile wild peas were never found in Afghanistan. Moreover, pea belongs to the Mediterranean floristic complex. The eastern border of the genus *Pisum* natural range most probably coincides with the border of Khorasan Subprovince of Iranian-Anatolian, or Armeno-Iranian Floristic Province and Turkestanian Floristic Province (Zohary, 1973; Takhtajan, 1978). This border has a nearly meridional direction and goes along the Sistan-Gerirud Depression between the mountains of Kopet-Dagh and Khorasan from one side and Kugitangtau (the Pamir-Alay Mountain System), Paropamise and Central Afghan Mountains (sometimes attributed to the Iranian Upland why in fact they are western foothills of the Hindukush) on the other side. This border well coincides with the eastern state border of Iran. Meanwhile, the most ancient archaeological sites containing the pea are in Levant (Fuller et al., 2011, 2012). Thus, Afghanistan by no means was the centre of pea domestication. N.I. Vavilov’s point of view about coincidence of the centres of diversity and domestication was criticised still during his life (Shlykov, 1936, 1937); nowadays it is in generally abandoned (Harlan, 1992; Goncharov, 2014) and is true only in cases when domestication by chance took place in the centres of genetic diversity of a species in nature, as it was in the cases of wheat (Zhukovskiy, 1971; Goncharov et al., 2007). Perhaps Afghanistan, as situated at the crossroads of many cultural/historical and migrational waves, has accumulated pea diversity originated already under cultivation, that is for the last 10–12 thousand years. An input of some autochthonous wild forms into the gene pool of some traditional Afghan forms of the cultivated pea cannot be theoretically denied but requires proof, with such forms unknown from the region. Anyway, genetic diversity of wild peas in Anterior Asia strongly exceeds that of the cultivated peas in Afghanistan, although attracted insufficient attention and remains scarcely studied.

WILD FORMS IN THE LAST SYSTEM OF THE GENUS *Pisum* L.

To avoid discord and misunderstanding, further on we will keep the last published system of the genus by N. Maxted and M. Ambrose (Maxted and Ambrose,

2001), even if the authors of the sources cited kept to other taxonomic treatments. Regrettably, authors of reviews and experimental papers involving heterogeneous materials as a rule choose the other “strategy” and uncritically reproduce taxonomical concepts of their sources, thus maintaining and increasing the existing confusion. The system by Maxted and Ambrose (2001) is very simple, that is the best solution in view of the complicated structure and insufficient knowledge of variation in the genus *Pisum*, which scarcely fits the traditional botanical classification with the hierarchical system of subordinate taxa. In general, this system follows the treatments earlier suggested by Townsend (1968) and Davis (1970). This system accepts three species:

1. *Pisum fulvum* Sibth et Smith.—morphologically a clear-cut wild species accepted by all researchers, ranging in Levant and probably entering Asia Minor and Arabia (Govorov, 1937; Makasheva, 1979).

2. *Pisum sativum* L., showing a great morphological and genetical variation. As a wild plant it ranges over a vast territory of the Mediterranean and Anterior Asia, and is cultivated worldwide as a crop. The system by Maxted and Ambrose assumes two subspecies, wild and cultivated. The cultivated forms are attributed to the subspecies *P. sativum* L. subsp. *sativum*, while all wild forms are united into the subspecies *P. sativum* L. subsp. *elatius* (Bieb.) Asch. & Graebn. sensu lato (the problem of the authority of this taxon in the subspecific rank is disputable, see Makasheva, 1979; Kosterin, Bogdanova, 2008). Low wild plants, earlier considered as the species *P. humile* Boiss et Noë (this name is a junior homonym of *P. humile* Miller) or subspecies *P. sativum* L. subsp. *syriacum* (Boiss et Noë) Berger, are considered in the system by Maxted and Ambrose as the variatio *P. sativum* L. subsp. *elatius* var. *pumilio* (Boiss et Noë) Meikle, following Davis (1969). Such a subspecific subdivision with the wildness/domestication as the only diagnostic character does not take into account existence of many phyletic lineages among wild representatives of the species (Kosterin and Bogdanova, 2008; Zaytseva et al., 2012), yet it is a convenient practical compromise putting aside a complicated problem of working out a phylogenetically justified classification of the species (Kosterin, Bogdanova, 2008).

3. *Pisum abyssinicum* A. Br. (in some other classifications regarded as the subspecies *P. sativum* subsp. *abyssinicum* (A. Br.) Berger)—a genetically very uniform taxon endemic for Ethiopia and Yemen, morphologically similar to *P. sativum* and in fact being one of the phyletic lineages of the latter which acquired a strong reproductive isolation. (Acceptance of the specific status of *P. abyssinicum* makes the species *P. sativum* paraphyletic, that does not fit the principles of a strict phylogenetic classification, the cladistics.) This taxon is known as cultivated while mentions of its existence in the wild in literature (Govorov, 1937;

Makasheva, 1979) are dubious, most probably they are a chain of repeated old speculations unjustified by data.

CRITERION OF WILDNESS

In spite of a widespread opinion, almost each pea form may be unequivocally classified as either wild or cultivated by the only key character, spontaneous dehiscing of pods (Waines, 1975; Ladizinsky, 1979; Weeden, 2007; Ambrose and Ellis, 2008; Kosterin et al., 2010). Upon becoming ripe, the pod walls of wild peas spontaneously open along the upper suture and immediately coil along their long axis in a spiral manner, so that open pods have a characteristic V-like appearance (figure). By this coiling impetus, the ripen seeds are shot to long distance, up to 360 m (Ambrose and Ellis, 2008). The pods of cultivated forms either do not dehisce at all or at high temperatures open much later, with weak or none coiling of the pod walls so that the seeds are not shot. The pod dehiscence is determined by a (semi)dominant allele of gene *Dpo* (*Dehiscing pod*) (Marx, 1971). An additional locus *Dpo2* was also reported (Weeden et al., 2002; Ambrose and Ellis, 2008). Although there is some variation with respect to the dehiscence strength (Ambrose and Ellis, 2008), classification of any pod as dehiscing versus non-dehiscing is doubtless. In our studies in pea genetics which have been being carried out since 1980s until now, we did not face intermediate states of this character. In particular, in conditions of the greenhouse of the Institute of Cytology and Genetics SB RAS, the first generation hybrids between wild and cultivated peas always had dehiscing pods, that is the corresponding alleles appear dominant. The two accessions of *P. sativum* subsp. *elatius* with non-dehiscing pods, JI199 and JI2201 (= VIR1947) from Israel and Krasnodarskiy Kray of Russia, respectively, reported by Ambrose and Ellis (2008), according to this characters must not be attributed to the said taxon (Kosterin et al., 2010).

The pod dehiscing is of a crucial importance, since it is associated with the opposite propagation strategies of wild and cultivated forms: the former face a problem of dispersal in nature and solve it ballistically, while the latter “wait for a harvester” (Waines, 1975; Ladizinsky, 1979; Weeden, 2007). Hence the plants with non-dehiscing pods cannot propagate in nature while those with dehiscing pods cannot be effectively cultivated. In this situation, disruptive selection operates which preserves wild forms to remain wild and cultivated forms to remain cultivated (Glémin and Battailon, 2012). Thus, even progenies of spontaneous crosses between cultivated and wild forms (which are possible) at once become either cultivated or wild plants depending on their genotype for *Dpo* and join the respective gene pools.



Withered plant of wild pea *Pisum sativum* subsp. *elatius*, with open pods, on a hill slope of the left bank of the Angueira River 1.4 km NE of Uva village, Vimioso Municipality, Trás-os-Montes e Alto Douro Province, Bragança District, Portugal, 8 July 2010 (photo by the author).

POTENTIALLY ECONOMICALLY VALUABLE TRAITS OF WILD PEAS

Genetic diversity of wild peas can be valuable for breeding first of all in the following directions:

- (1) resistance to pests and a broad spectrum of pathogens (considered in detail below);
- (2) resistance to abiotic stress, first of all to extreme temperatures (Ali et al., 1994; Coyne et al., 2011);
- (3) nutritional and fodder value (North et al., 1989; Domoney et al., 1991; Bastianelli et al., 1998; Heng et al., 2006);
- (4) agrotechnical advantages, such as branching (Murfet and Reid, 1993), ability to hibernate;
- (5) peculiarities of symbiotic nitrogen fixation.

The amount of data obtained for each of these items decreases according to the above order. The best studied is the issue of resistances.

P. fulvum was shown to be resistant to the pea weevil (*Bruchus pisorum* L.) (Clement et al., 2002, 2009; Byrne et al., 2008; Aryamanesh et al., 2012, 2014), rust (Barilli et al., 2009, 2010), powdery mildew (a complete resistance) (Fondevilla et al., 2007b) and ascochyta blight (Wroth, 1998; Fondevilla et al., 2005; Carrillo et al., 2013).

The pod walls of *P. sativum* subsp. *elatius* s.l., as well as of most traditional landraces of *P. sativum* subsp. *sativum* originating from the Balkans and Anterior Asia, react to the pea weevil oviposition by formation of callus-like outgrowths of epidermis cells, sometimes able to mechanically throw the egg away (Berdnikov et al., 1992). For the first time this reaction was described in a cultivated pea by Vilkova et al. (1977). It is noteworthy that this phenomenon does not take place in *P. fulvum* (Berdnikov et al., 1992), the resistance of which to the weevil is achieved by other means.

Some wild forms of the cultivated pea (*P. sativum* subsp. *elatius*) showed resistance to the nematode *Heterodera goettigniana* Liebscher (Vito and Perrino, 1978), broomrape *Orobanche crenata* Forsk. (Valderama et al., 2004), powdery mildew (Fondevilla et al., 2007a, 2008, 2011), *Fusarium* wilt (McPhee et al., 1999; Hance et al., 2004), ascochyta blight (Fondevilla et al., 2005; Carrillo et al., 2014) and white mould, caused by *Sclerotinia sclerotiorum* (Lib.) de Bary (Porter et al., 2009).

Wild forms are also considered as promising genetic resources useful to overcome abiotic stress: *P. fulvum* shows a fast and deep growth of roots, in some *P. sativum* subsp. *elatius* the transpiration is lowered, while accession J12055 from Italy, belonging to this taxon, remains viable at low temperatures up to and—20°C (Ali et al., 1994).

It would seem that wild peas can be useful with respect to the pre-existing genetical diversity for selection towards intensified symbiotic nitrogen fixation. This issue was studied by T.A. Lie with colleagues (Lie, 1978, 1981, 1984; Lie et al., 1987). Their results showed that selection for this character using wild forms would be complicated by a problem of compatibility of a plant and its bacterial symbiont, and would demand non-trivial approaches if at all possible. The cited authors revealed a considerable coevolution of pea forms and *Rhizobium leguminosarum* strains leading to coherent regional divergence of both. Thus, only Israeli rhizobium strains were able of symbiosis with *Pisum fulvum*, only strains from the soils of Anterior and Central Asia were able of symbiosis with a primitive pea form from Afghanistan, and a pea lineage was found in southern Turkey which was unable of symbiosis with rhizobium strains from other regions of this country (Lie, 1981; Lie et al., 1987). In general, the strains from the soils of Afghanistan, Turkey and Israel showed a broad specificity and induced nodulation in most forms of *Pisum sativum* while European strains appeared compatible with only some fraction of Asian cultivated peas (Young and Matthews, 1982; Young et al., 1982). This is not surprising since Anterior Asia is a birthplace of the cultivated pea. It is not excluded that the European strain was initially pre-existing in nature as a symbiont of local legume species (as it actually is) while pea forms compatible with it were automatically selected while penetrating of the pea culture to Europe (Young and Matthews, 1982). So, if forms with increased nitrogen fixation were found among wild peas (that still did not happen), their involvement in breeding would demand a simultaneous involvement of useful genes of both plant and bacterial symbionts, including cultivation of the resulted crops only in regions where the respective rhizobium strain is present, or agrotechnical procedures of inoculation of soils with certain bacterial strains (Borisov et al., 2011).

GENETIC ANALYSIS OF ECONOMICALLY USEFUL TRAITS OF WILD PEA FORMS

Some modest advances were achieved towards the use of genetic diversity of wild pea forms in breeding. One can still speak about getting promising genotypes, that is about pre-breeding. The first stage is a genetic analysis of economically useful traits. *P. fulvum* is known to be resistant to pea weevil associated with mortality of its larvae on the pod surface just after hatching, inside pod walls and inside seeds (Clement et al., 2009). An Australian team carried out a genetic analysis of resistance to weevil of the developing seeds (not of the pod walls) in three generations of hybrids of *P. fulvum* and *P. sativum* and concluded that it is tri-genetically controlled (with the 1 : 63 ratio of phenotypes) by simultaneous presence in three different loci of recessive alleles from *P. fulvum* in homozygous state (Byrne et al., 2008). This mode of inheritance implied that the seed resistance to the weevil could be transferred to the cultivated peas by backcrossing but would be laborious and demanding involvement of numerous hybrid populations. At the same time an American team (Clement et al., 2009) found out a considerable resistance to weevil in not so numerous populations of the second and third generations of hybrids of *P. sativum* and *P. fulvum*, achieved by traits of the pod walls, in particular affecting behaviour of the just hatched larvae (immediate penetration inside the pod wall versus crawling over the surface).

Later the Australian team applied to the second generation of their hybrids the QTL analysis—a procedure aimed to reveal loci with quantitative effect (QTL) basing of linkage of that effect to certain regions of the genetic map—and discovered a quite far more complicated inheritance pattern (Aryamanesh et al., 2014). Three major and five minor QTLs were responsible for 95% of variation for the resistance because of larval mortality in cotyledons, three major (two of which linked to each other) and two minor QTLs were in sum responsible for 70% of variation for resistance because of inability of the larvae to penetrate inside seeds through their cover and just one QTL provided 8.8% of variation for inability of the larvae to penetrate inside pods. Thus the earlier data by Byrne et al. (2008) on inheritance of the resistance at the level of the larval penetrability into seeds were confirmed. Note that the revealed QTLs were not QTLs in a strict sense because their effect was strongly affected by domination and gene interaction.

The callus-like neoplastic outgrowths on the pod wall surface in response to the pea weevil ovipositions are determined by presence of a dominant allele *Np* (*Neoplastic pod*) (Berdnikov et al., 1992). This gene was well known before because of its harmful by-side effect of spontaneous formation of such outgrowths, sometimes very intensive, on pod walls in the greenhouse conditions (that is in absence of the ultra-violet radiation and at high humidity). In the above cited

work it was shown that in the outdoors conditions, these outgrowths are induced by oviposition and are adaptive as a factor of resistance to weevil. Later the physiology of this phenomenon was studied in detail by an American team headed by Robert Doss (Doss et al., 2000; Oliver et al., 2000, 2002; Cooper et al., 2005; Doss, 2005) who even announced a special class of organic substances—bruchins (Schultz et al., 2001),—as present in a secret by a beetle female and inducing the neoplasia (naturally, one should not believe that this is a ‘biological role’ of these substances, since the neoplasia is undesirable for the beetle). It should be noted however that according to the unpublished data by V.A. Berdnikov’s team, in outdoors conditions the neoplasia could be induced by quite diverse organic substances, so naming some of their class ‘bruchins’ seems to be not so reasonable.

In *P. fulvum*, a dominant gene was discovered which brings about resistance to the powdery mildew caused by *Erysiphe pisi*, which was not allelic to the two genes with a similar effect known in *P. sativum* (Fondevilla et al., 2010). In progenies of the second generation hybrids from a cross of another accession of *P. fulvum* with *P. sativum*, the same team located one QTL responsible for 63% of variation for partial resistance to rust (Barilli et al., 2010), that is a convenient situation for introduction of this character to the cultivated pea.

A predominantly Spanish team took a fancy to accession P665 of *P. sativum* subsp. *elatius* as a source of resistance to a number of parasites such as *Orobancha*, *Ascochyta* and *Pseudomonas*. Analysis of the third generation hybrids from its cross with a cultivated pea revealed two QTLs responsible for resistance to broomrape (Valderrama et al., 2004). Genetic analysis with the use of a series recombinant inbred lines (RIL) from that cross revealed the same number of QTL responsible for resistance to bacterial blight (Fondevilla et al., 2012). A preliminary analysis of the same RIL population showed presence of seven QTLs responsible for resistance to ascochyta blight (Fondevilla et al., 2007a), while a finer analysis with involvement of additional SNP raised the number of such QTLs to 16, which affected different aspects of the resistance, and allowed to suggest candidate genes for some of them (Fondevilla et al., 2008, 2011; Carillo et al., 2014).

Compatibility of different pea forms and *Rhizobium leguminosarum* strains have been a subject of numerous works on simultaneous genetic analysis of both symbionts so that the genetic and molecular nature of interaction of these plant and bacterial symbiont are studied in detail (Borisov et al., 2011). Note that these works involved European cultivars, mutants obtained at their basis, and “primitive” locally cultivated landraces unaffected by conscious selections, in particular from Iran, Afghanistan, Tibet and India (Kneen and LaRue, 1984), but not wild pea forms. A special attention was paid to the so-called “cultivar Afghani-

stan” (accession JI1357), introduced into research by T.A. Lie (1971, 1978, 1984), which is unable of nodulation at inoculation with European rhizobium strains.

Just one work related to the prospect of the use of wild pea forms in breeding advanced beyond claiming useful traits and studying their inheritance. Aryamanesh et al. (2012) chose a fifth generation hybrid from a cross of a cultivated pea with *Pisum fulvum*, once backcrossed it to the cultivated pea and then carried out five generations of selection in favour of resistance, which resulted in five resistant lines. By this, transgression of resistance of *P. fulvum* to *P. sativum* was carried out. These five lines comprise a material perspective for breeding. Note that they still carried too large share of the *P. fulvum* genome (a quarter was theoretically expected).

OBJECTIVE AND SUBJECTIVE CONSTRAINTS OF THE USE OF WILD PEA FORMS IN BREEDING

These above mentioned works were considered here in detail since they actually exhaust the first steps made towards the use of wild peas in breeding. Thus, until recently the resource of pea natural genetic diversity remained, first, unclaimed. Second, it is still too scarcely studied. Germplasm collections of the world contain just about 100 accessions of wild peas which were repeatedly doubled and acquired new designations while seed exchange, so that the same accession may exist in the same collections under different numbers and even return to the initial collection under a new number. Moreover, this material was under risk of spontaneous crossing with other genotypes while being reproduced, the traces of which we observed in seed samples obtained from different collections (e.g. in the All Russian Plant Breeding Institute, St. Petersburg, Russia, and Weisbullholm collection, Landscrona, Sweden). Long ago collected accessions often lack sufficient information on their origin and have only very general provenance such as “Palestine” or “Abyssinia”. Only recently a deserved interest appeared in as broad as possible collecting of material of wild relatives materials of peas as well as other crops (Maxted and Kell, 2009; Maxted et al., 2012). Quite symptomatic is the title of a review article by 20 experts worldwide published in 2011 in *BioScience*: “Crop wild relatives—undervalued, underutilized and under threat?” (Ford-Lloyd et al., 2011, p. 559). In this view, the international organisation Global Crop Diversity Trust arranged a number of expert consultations on wild relatives of each basic crop. The consultation of pea crop wild relatives took place on September 30–October 1, 2014 at John Innes Centre in Norwich, UK; in which the author of this paper participated. Unfortunately, a summarising paper on its results still did not appear.

It should be said that the use of natural pea diversity in breeding is hampered by reproductive barriers exist-

ing not only between different species of pea but even within *P. sativum*. Under “reproductive barriers” we imply here a complete or partial sterility for seeds and/or pollen of the first generation hybrids, and in some cases impossibility of obtaining such hybrids (Kosterin and Bogdanova, 2014). There are data that reproductive barriers between *P. sativum* and other species of the genus, *Pisum fulvum* and *P. abyssinicum*, at least in part are because of reciprocal translocations (Ben-Ze'ev and Zohary, 1973; Conicella and Errico, 1990; Errico et al., 1991) which impair meiosis in heterozygous state in hybrids, that is affect fertility of the first generation hybrids. Karyological analysis of meiosis in the first generation hybrids allowed to suppose that at least one translocation participates in reproductive barriers inside the species *Pisum sativum* as well (Ben-Ze'ev and Zohary, 1973). However, the role of translocation in reproductive isolation in peas is overestimated since the pollen semisterility and even abnormalities in bivalent pairing can result from the conflict of the nucleus and plastids (Bogdanova and Galieva, 2009; Bogdanova et al., 2012, 2014) and may not only be phenotypic manifestations of heterozygosity for reciprocal translocations (Lamm, 1951) to which they used to be ascribed.

One more, and quite unexpected a problem of the use of wild pea forms is insufficient knowledge on their diversity in those who attempt this use, and first of all on the taxonomy of the genus *Pisum* and its problems. As a rule, taxonomy is accepted by geneticists and breeders uncritically, and they tend to overestimate its reliability in assuming taxa quite homogenous inside them and at the same time quite distinctly separated from each other, so that any classified specimen well represent its taxon (that is too far from reality). As a rule, researchers often do not take into account geographical provenance of accessions with which they work. O.E. Kosterin and V.S. Bogdanova (2014) called this approach a “taxonomical trap”.

For instance, in the papers by the Spanish team which studied in detail the genetics of resistance of accessions P665 (by the way this is just an internal designation used by this team) to different pathogens and pests (Valderrama et al., 2004; Fondevilla et al., 2007a, 2008, 2012; Carillo et al., 2014) there is no any indication of the origin of this accession. Only the paper by Fondevilla et al. (2005) mentions that it was received from the ICARDA collection. It turned out that this accession was initially identified in that collection as *P. fulvum*, correctly reidentified by the mentioned authors as *Pisum sativum* subsp. *syriacum* (in the here accepted system by Maxted and Ambrose this taxon corresponds to *P. sativum* subsp. *elatius* var. *pumilio*), but they did not further look for its origin since they assumed it to be a “typical representative” of this subspecies (pers. comm. by D. Rubialis). In fact this taxon is very heterogeneous in any of its accepted volumes. Not without a difficulty and with involvement of unpublished catalogues, it was possible to find out that

this was the ICARDA accession IG52439 collected on May 5, 1986 in Syria, Damascus Province, at a locality with the latitude 33,62111 N, the longitude 36,03028° E and elevation 1,110 m above sea level (according to the ICARDA database), that is at Lake Zarzar in Shir Mansur Mts.; in other collections this accession is also designated as 868313, 142-2810 and WG 17093.

Accession PI269818 was honoured to be the second genotype for which the BAC clone library has been created. However, its origin and taxonomical attribution was not mentioned neither in the paper devoted to the creation of that library (Coyne et al., 2007) nor in the papers referenced therein. Only the works by R. Provvidenti with colleagues (Provvidenti, Alconero, 1988; Provvidenti, Hampton, 1993) there is indication that it “originates from the USSR”!

An oppressive example of confusion because of geneticists' disregard of knowledge of the material they work with is the fact that the ‘cultivar Afghanistan’ (JI1357), a primitive pea from Afghanistan involved into scientific research by T.A. Lie (1978, 1984), was later simultaneously mentioned both as “cv. Afghanistan” and as “wild pea variety Afghanistan” (Geurts et al., 1997). Earlier Yang and Matthews (1982) had studied this germplasm specially. They found out that lineages from Afghanistan which are resistant to the European strain of *Rhizobium* (the symbiotic nitrogen fixing bacterium) are phenotypically very similar to each other: they have small flowers of muddy coloration because of flavonoid pigmentation of the corolla, small seeds with a marble pattern, they miss anthocyanin coloration on vegetative organs and are resistant to ascochyta blight. Yang and Matthews called this appearance (not the peas themselves) “wild” only in a metaphorical sense! On the other hand, Afghan accessions sensible to the European *Rhizobium* exhibited far broader diversity. The phenotype of the group of resistant accessions best fits to the subspecies *P. sativum* subsp. *asiaticum* Govorov isolated by L.I. Govorov (1928). However, most of very diverse primitive cultivated peas from Asia and even North Africa were later included into this subspecies (Govorov, 1937), so that in general the Asian subspecies can hardly be regarded as actually existing (Maxted and Ambrose, 2001). Yang and Matthews recognised some phenotypically resemblance of the resistant Afghan accessions with accession JI241 from Jerusalem, identified as “*Pisum humile*” and also resistant to the European rhizobium strain. However, all resistant Afghan accessions represent a traditional locally cultivated form—they originate from markets all over Afghanistan, while their pods do not dehisce (Yang and Matthews, 1982). Nobody ever register a wild pea in Afghanistan, while from biogeographical considerations it can hardly be present there. However, directional search for wild peas in the flora of Paropamisia (north-western Afghanistan) would be quite welcome.

All the above considerations stress the actuality of comprehensive and detailed investigation, involving

all available information, first of all geographical and genetical, of wild representatives of the genus *Pisum* and reconstruction of an adequate picture of both its contemporary structure and the history of its divergence and propagation. Bringing this subject in order is not even timely but rather belated, since ignorance of provenance and confusion in taxonomic attribution of the material long became bad traditions. One should not disregard the current disappearance of wild pea natural habitats of because of transformation and degradation of plant communities because of direct (agriculture, construction) and indirect (global warming) human influence. The tempo of that vanishing is unknown but most probably high. We cannot afford ourselves to loose time in study and preservation of wild pea in our so fast changing world.

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CONFLICT OF INTERESTS

The author claims there is no any conflict of interests.

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